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Effectiveness of Six Potential Irritants on Consumption by Red-Winged Blackbirds *(Angelaius phoeniceus)* and Starlings *(Sturnus vulgaris)*

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The morphological organization of the peripheral trigeminal system in birds is not very different from that in mammals, but there appear to be broad functional (e.g., behavioral) discrepancies. The present experiments were designed to explore these behavioral discrepancies by testing avian responsiveness to a variety of potent mammalian irritants. In experiment 1 red-winged blackbirds (*Agelaius phoeniceus*) and starlings (*Sturnus vulgaris*) were assigned to 12 groups. Interspecific group pairs were presented with allyl isothiocyanate, ammonia, gingerol, mercaptobenzoic acid, piperine, or zingerone at five concentrations [0.0, 0.001, 0.01, 0.1, 1.0% (w/w)] in randomized, 2-hr, one-choice tests. The design of experiment 2 was similar to that of experiment 1, except that only allyl isothiocyanate, mercaptobenzoic acid, and piperine served as stimuli, and a broader concentration range of each stimulus [0.0-10.0% (w/w)] was used. In experiment 3, allyl isothiocyanate, mercaptobenzoic acid, and piperine again served as stimuli and concentrations again ranged from 0.0 to 10.0% (w/w), but different group pairs were tested with different concentrations of individual irritants in a double changeover design. The results of experiments 1 and 2 showed that allyl isothiocyanate, mercaptobenzoic acid, and piperine reduced consumption at high ($\geq$1.0% w/w) concentrations. Ammonia, gingerol, and zingerone were ineffective. In contrast, the results of experiment 3 suggested that even the lowest concentration [0.001% (w/w)] of allyl isothiocyanate, mercaptobenzoic acid, and piperine were aversive. As such, while different experimental designs were consistent in the feeding responses elicited, apparent sensitivity was influenced by habituation and/or sensitization. We propose that changeover designs (experiment 3) are preferable to simple randomized stimulus presentations (experiments 1 and 2). We speculate that irritants may have practical uses as bird control compounds and as adjuvants to registered repellents in specialized settings.

I. INTRODUCTION

In higher vertebrates, an important component of the common chemical sense (Parker, 1912) is the trigeminal system. This system consists of free nerve endings in the exposed surfaces of the eye, mouth, and nose. While the morphological organization of the peripheral trigeminal system in birds is not very different from that in mammals (Dubbledam and Veenman, 1978), there appear to be broad functional discrepancies (Kare and Mason, 1986; Mason et al. 1988). For example, the avian trigeminal system is responsive to odorants (e.g., Walker et al., 1979; Mason and Silver, 1983) but apparently does not mediate avoidance of strong mammalian irritants. Thus, pigeons (*Columba livia*) and gray partridges (*Perdix perdix*) are indifferent to ammonia (Soudek, 1929), and parrots (*Amazona* spp., Mason and Reidinger, 1983), pigeons (Szolcsanyi et al., 1986), and red-winged blackbirds (Mason and Maruniak, 1983) are insensitive to capsaicin, the pungent principle in *Capsicum* peppers.

The present experiments were designed to assess the responses of two passerine species (red-winged blackbirds [*Agelaius phoeniceus*], European starlings [*Sturnus vulgaris*]) to several potential irritants. In experiments 1 and 2, interspecific group pairs were presented with different chemicals (one chemical per pair) at a variety of concentrations. In experiment 3, interspecific group pairs were presented with all chemicals, but at only one of six concentrations. Two different paradigms were employed because pilot experiments had suggested that the responses of passerines to chemical irritants might be context-specific (i.e., "sensitivity" might depend on the method of stimulus presentation).

The irritants used were allyl isothiocyanate, ammonia, gingerol, mercaptobenzoic acid, piperine, and zingerone. Allyl isothiocyanate is the pungent principle in black mustard (*Brassica niger*), and recent evidence indicates that it is aversive to pigeons (Szolcsanyi et al., 1986). Ammonia is a prototypical trigeminal stimulus and reports suggest that passerines in feed lots avoid livestock diets containing high levels of nonprotein nitrogen (e.g., ammonia). Mercaptobenzoic acid was tested because of its commercial use in South Africa as an avian repellent (J. Thorpe, DuPont Co., pers. commun.). Gingerol and zingerone are the pungent components of ginger (*Zingiber officinale*) and piperine is the pungent component of black pepper (*Piper nigrum*).

II. MATERIALS AND METHODS

A. Experiment 1

Thirty-six experimentally naive male red-winged blackbirds (*Agelaius phoeniceus*) and 36 starlings (*Sturnus vulgaris*) served. All birds were individually caged (dimensions: 61 × 36 × 41 cm) under a 6:18 light-dark cycle (Mason and Reidinger, 1982). Water was always available, and before adaptation to experimental conditions the birds were permitted free access to Purina Flight Bird Conditioner (PFBC) and crushed shell grit.

Allyl isothiocyanate (Flavor Innovations, South Plainfield, NJ), piperine (ICI Biomedicals, Inc.), gingerol (PPF International, East Hanover, NJ), ammonia (Sigma), mercaptobenzoic acid (Sigma), and zingerone (Pfaltz and Bauer) were dissolved in 10 ml of ethanol, and then these solutions were mixed with PFBC to produce concentrations of 0.001, 0.01, 0.1, and 1.0% (w/w).

Five days before the experiment, all birds were adapted to a food deprivation regime. Deprivation involved removing all food and grit from the cages at dark onset. At light onset of the following day, 20 g of PFBC was placed in each cage. After 2 hr, consumption was assessed, and the birds were permitted free access to food and water until lights out.

On day 6, birds were assigned to 12 groups (six groups per species) on the basis of consumption. Briefly, the bird with the highest consumption was assigned to group 1, that with the second highest to group 2, and so on. This assured that the groups were balanced with respect to mean consumption.

The 12 groups were randomly assigned to six interspecific group pairs. Each pair was presented with five concentrations [0.0, 0.001, 0.01, 0.1, 1.0% (w/w)] of a different randomly selected irritant in a series of 2 hr no-choice tests. Over the next 15 days, presentations of each concentration were randomized such that each was presented three times. At the end of each 2 hr test, consumption was assessed, and birds were offered plain PFBC until lights out when food was removed.

After all tests had been given, mean consumption by each bird in each group for each irritant concentration was calculated. These means were assessed in a three-factor analysis of variance (ANOVA; irritants, species, concentrations), with repeated measures over concentrations. Tukey Honestly Significant Difference (HSD) tests were used to isolate significant differences among means.

B. Experiment 2

Eighteen experimentally naive male red-winged blackbirds and 18 starlings served. These birds were caged, maintained, and adapted to a food deprivation regime as previously described. Each species was assigned to three groups on the basis of consumption, and the groups were randomly assigned to three interspecific group pairs.

On the basis of experiment 1 results, only allyl isothiocyanate, mercaptobenzoic acid, and piperine served as stimuli. Experiment 2 essentially served as a replication of experiment 1, except that a broader range of stimulus concentrations was used. Different group pairs were randomly assigned to a single irritant, presented at six concentrations [0.0, 0.001, 0.01, 0.1, 1.0, 10.0% (w/w)] in a randomized series of 2 hr, no-choice tests. Mean consumption by each bird in each group for each irritant concentration was calculated and these means were assessed in a three-factor ANOVA (irritant, species, concentration), with repeated measures over concentration. Tukey HSD tests were used to isolate significant differences among means.

C. Experiment 3

Thirty-six experimentally naive male red-wings and 36 starlings were assigned to 12 groups ($n = 3$/group for each species) on the basis of consumption, as previously described. The groups were assigned to six interspecific pairs, and the pairs were randomly assigned to one of six concentration levels [0.0, 0.001, 0.01, 0.1, 1.0, 10.0% (w/w)]. At each of these levels, group pairs were given 2 hr, no-choice tests among allyl isothiocyanate, mercaptobenzoic acid, and piperine according to a double-changeover design (Heisterberg and Otis, 1983; Table 1).

Unlike experiments 1 and 2 in which stimulus presentations were randomized, the double-changeover design balanced presentations so that all irritants preceded and followed one another an equal number of times. As such, the design permitted estimation of residual and direct treatment effects, although the effective number of replicates for the former was less than the number for the latter (Federer, 1955).

An ANOVA procedure tailored for a three-treatment, double-changeover design (Federer, 1955) was used to assess the results. Tukey HSD post-hoc tests were used to isolate significant differences among means.

TABLE 1 Double-Changeover Design for Stimulus Presentations

	Square 1[b] bird			Square 2 bird		
Presentation[a]	1	2	3	1	2	3
1	A[c]	B	C	A	B	C
2	B	C	A	C	A	B
3	C	A	B	B	C	A

[a]Repeated for each concentration level.
[b]The two groups of three birds each are randomly assigned to the two Latin squares.
[c]A = piperine; B = mercaptobenzoic acid; C = allyl isothiocyanate.

III. RESULTS

A. Experiment 1

There were significant differences among irritants ($F(5,60) = 16.95$, $p < 0.00001$), between species ($F(1,60) = 813.82$, $p < 0.00001$), and among concentrations ($F(4,240) = 73.98$, $p < 0.00001$). Also, there were interactions between irritants and species ($F(5,60) = 8.29$, $p < 0.00001$), irritants and concentrations ($F(20,240) = 73.98$, $p < 0.00001$), and species and concentrations ($F(4,240) = 20.34$, $p < 0.00001$). Finally, the three-way interaction among irritants, species, and concentrations was significant ($F(20,240) = 9.20$, $p < 0.000001$).

Tukey tests ($p < 0.01$) indicated that overall, (a) allyl isothiocyanate and piperine reduced consumption relative to the other irritants, (b) red-wings exhibited lower consumption than starlings, and (c) consumption was lowest at the highest irritant concentration.

Post-hoc examination ($p < 0.01$) of the irritant by species and species-by-concentrations interactions suggested that allyl isothiocyanate, mercaptobenzoic acid, and piperine produced greater drops in consumption by starlings than by red-wings. In addition, while both 0.1 and 1.0% concentrations of irritant reduced consumption by starlings, red-wings were affected only by the latter.

Post-hoc examination ($p < 0.01$) of the irritant by concentration interaction indicated that only the highest concentration of allyl isothiocyanate and mercaptobenzoic acid reduced consumption. Piperine appeared to be more effective and significantly reduced consumption at both 0.1 and 1.0%.

Finally, post-hoc examination ($p < 0.01$) of the interaction among irritants, species, and concentrations reinforced inferences drawn on the basis of the main effects and lower order interactions (Fig. 1). While red-wings and starlings exhibited the same pattern of consumption across concentrations,

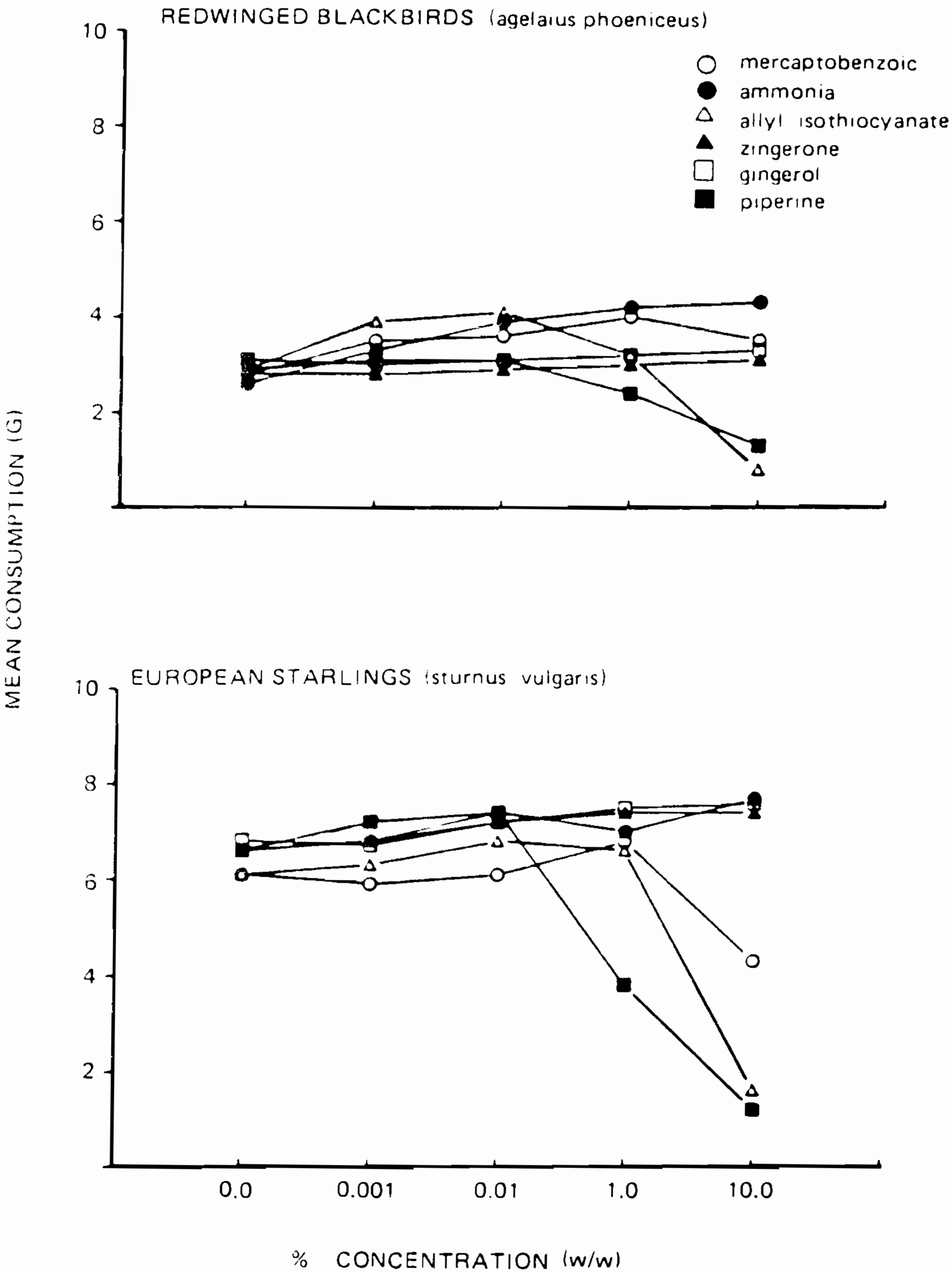

FIGURE 1 Mean consumption of irritant adulterated PFBC in experiment 1 by red-winged blackbirds (top panel) and starlings (bottom panel).

starlings showed higher consumption than red-wings. Among irritants, only allyl isothiocyanate and piperine caused significant reductions in consumption for both species (Fig. 1), and this effect was observed only at concentrations equal to or exceeding 1.0%. Mercaptobenzoic acid significantly reduced consumption by starlings at a concentration of 1%, but feeding by red-wings was not similarly affected. Ammonia, gingerol, and zingerone had no effects on consumption by either species.

B. Experiment 2

There were significant differences among irritants ($F(2,30) = 6.11$, $p < 0.006$), between species ($F(1,30) = 179.14$, $p < 0.00001$), and among concentrations ($F(5,150) = 351.79$, $p < 0.00001$). In addition, there were significant interactions between irritants and concentrations ($F(10,150) = 28.23$, $p < 0.00001$) and species and concentrations ($F(5,150) = 71.37$, $p < 0.00001$). Finally, the three-way interaction among irritants, species, and concentrations was significant ($F(10,150) = 7.00$, $p < 0.00001$).

Tukey tests ($p < 0.01$) revealed that overall (a) allyl isothiocyanate and piperine were more aversive then mercaptobenzoic acid, (b) starlings showed higher consumption than red-wings, and (c) consumption was lowest at the highest [1.0 and 10.0% (w/w)] irritant concentrations.

Examination of the irritant-by-concentration interaction revealed that the lowest consumption of all irritants occurred at the 10% concentration. While there was no difference between consumption at 10.0 and 1.0% for allyl isothiocyanate or piperine, consumption of mercaptobenzoic acid increased significantly from the former to the latter. Consumption of all irritants increased when the concentration was reduced to 0.1%, although piperine consumption was significantly lower than consumption of allyl isothiocyanate or mercaptobenzoic acid. There were no differences in consumption at concentrations lower than 0.1%.

Examination of the species by concentration interaction suggested that as in experiment 1, starlings were more sensitive than red-wings to food adulterated with the higher irritant concentrations. For the three highest concentrations (0.1-10.0%), consumption by starlings was less than that by red-wings.

Examination of the three-way interaction among irritants, species, and concentrations reinforced inferences drawn on the basis of the main effects and lower order interactions. All three irritants were repellant at 10% (w/w), but only mercaptobenzoic acid was more aversive at 10% than at 1.0% (Fig. 2). Between species, red-wings showed lower consumption than starlings at concentrations between 0.0 and 0.1% (w/w). At 1.0-10.0%, there were no differences between species.

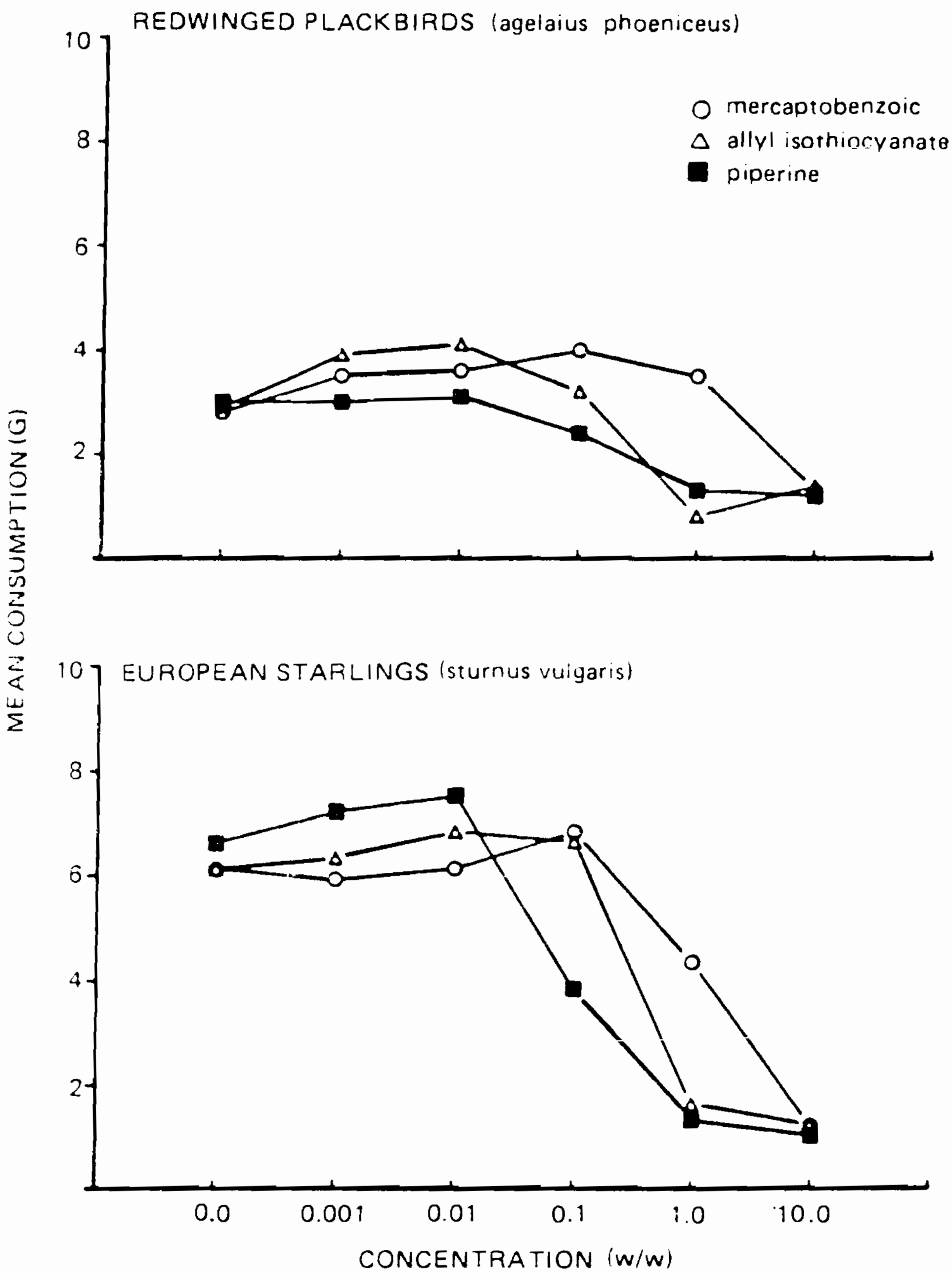

FIGURE 2 Mean consumption of irritant adulterated PFBC in experiment 2 by red-winged blackbirds (top panel) and starlings (bottom panel).

C. Experiment 3

The results of ANOVAs for each of the species/concentration combinations are summarized in Table 2. In general, factors associated with groups of birds, individuals within groups, and time periods were not significant, indicating that individual birds tended to be consistent in their response to treatment regimes as well as unaffected by repeated testing over a 3-day period.

TABLE 2 Summary of ANOVA Results in Experiment 3

Red-winged blackbirds

		F value concentrations					
	df	0	10^{-3}	10^{-2}	10^{-1}	1	10
Group	1,4	0.001	1.4	0.015	0.5	0.1	0.5
Period	2,4	**7.3**	0.3	0.6	0.3	2.5	0.9
Bird (group)	4,4	**9.9**	1.0	1.8	0.9	0.2	0.5
Period × group	2,4	2.9	1.9	2.8	0.2	2.0	0.5
Direct (ig. residual)	2,4	0.6	**43.0**	**27.0**	**18.0**	**12.8**	0.6
Residual (elim. direct)	2,4	2.1	2.9	0.7	0.6	0.02	0.4
Direct (elim. residual)	2,4	1.0	**37.2**	**19.5**	**14.2**	**10.4**	0.2
Residual (ig. direct)	2,4	1.7	**8.6**	**8.1**	4.4	2.4	0.8

Starlings

		F value concentrations					
	df	0	10^{-3}	10^{-2}	10^{-1}	1	10
Group	1,4	**30.1**	**7.5**	1.6	0.2	1.6	6.8
Period	2,4	2.7	3.3	1.7	1.2	0.3	0.5
Bird (group)	4,4	**30.1**	1.1	0.9	0.9	0.2	2.0
Period × group	2,4	0.3	0.3	0.03	1.1	0.05	1.8
Direct (ig. residual)	2,4	1.3	**181.8**	**22.1**	**38.9**	2.2	0.8
Residual (elim. direct)	2,4	0.5	**7.6**	0.8	**11.3**	0.3	5.3
Direct (elim. residual)	2,4	0.8	**175.1**	**18.5**	**36.6**	2.4	0.5
Residual (ig. direct)	2,4	1.0	**14.3**	4.4	**13.7**	0.1	5.6

Significant F values in bold type:

df	0.05	0.01
1,4	7.7	21.2
2,4	6.94	18.0
4,4	6.39	16.0

Because residual effects are somewhat confounded with individuals in this design, overall treatment effects can be broken out in two ways: (a) direct ignoring residual effects and residual eliminating direct effects, or (b) direct eliminating residual effects and residual ignoring direct effects. For practical purposes, emphasis is placed on the two terms that eliminate (adjust) direct effects for the residual effects, and vice versa. For both species, direct treatment effects, adjusted for residual, were revealed at the lowest concentration (0.001%) and continued through the 0.1% level. At the two highest concentrations, direct treatment effects dissipated, with the exception of red-wings at the 1.0% level. Examination of Figs. 3 and 4 show that these differences were due to the greater effectiveness of allyl isothiocyanate in reducing consumption. There is no evidence that mercaptobenzoic acid and piperine differed in their repellant activity. At higher concentrations, all three compounds were equally effective in reducing consumption.

Results from all 12 groups were combined and analyzed by computing a three-factor ANOVA (species, concentrations, treatments) on the adjusted treatment means from the individual groups. An overall experimental error mean square was calculated by averaging mean squares over experiments. The analysis produced strong evidence for overall differences among treatments ($F(2,48) = 23.06$, $p < 0.001$) and concentrations ($F(5,48) = 89.54$, $p < 0.001$). Tukey HSD tests ($p < 0.01$) indicated that piperine and mercaptobenzoic acid were not different, but allyl isothiocyanate was significantly better than both. Consumption at all concentration levels was significantly reduced from control levels. Further, any levels more than one order of magnitude apart were significantly different. There was a significant species by

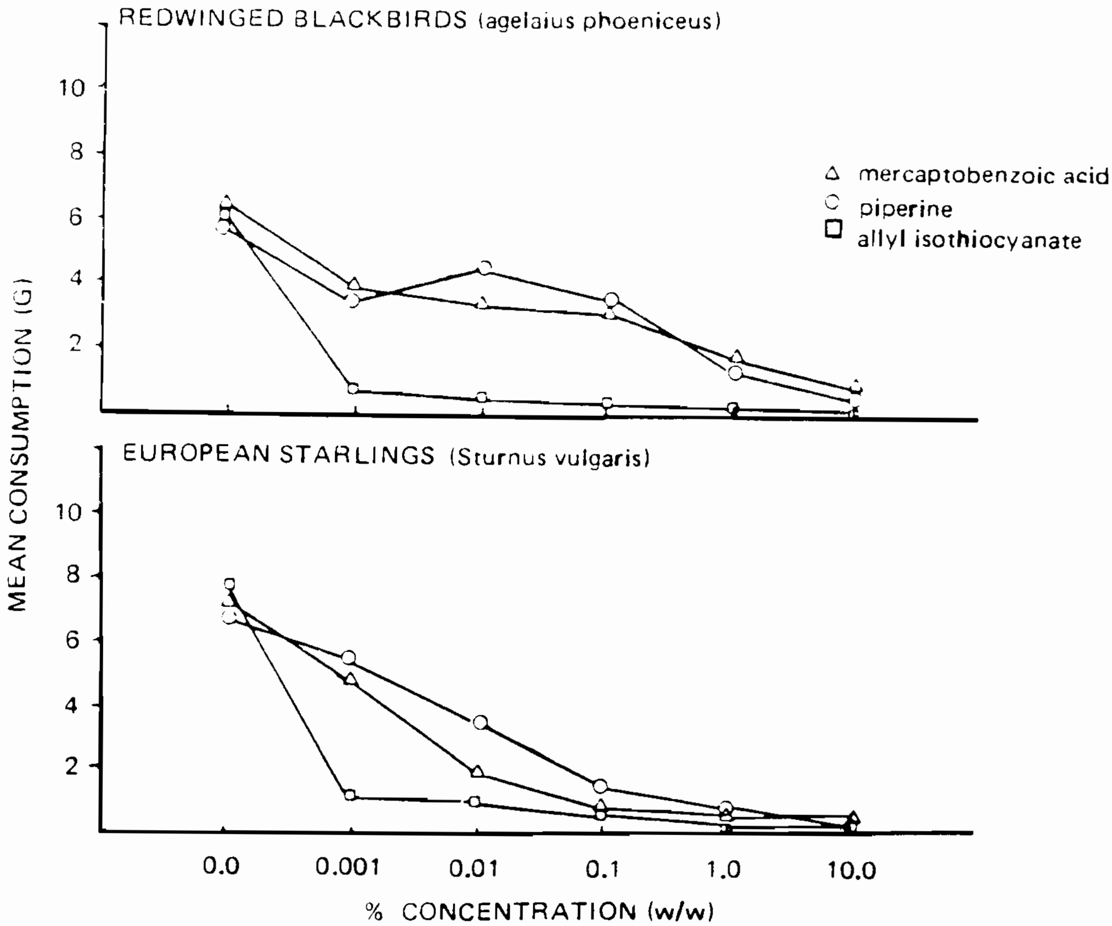

FIGURE 3 Mean consumption of irritant adulterated PFBC in experiment 3 by red-winged blackbirds (top panel) and starlings (bottom panel).

ation interaction (F(5,48) = 4.11, $p < 0.005$), due to the relative of the red-wing dose-response curve for medium concentration lev- perine and mercaptobenzoic acid (Fig. 3). The same phenomenon onsible for evidence of a concentration-by-treatment interaction = 4.24, $p < 0.001$).

eneral lack of significant residual effects exhibited in the individual nts is indicated in Table 2. Evidence for residual effects appeared two of the starling groups and for none of the red-wing groups. ge absolute adjustment in treatment means for residual effects was 7 g/period (s.d. 0.068).

USSION

ary goal of the present experiments was to assess the repellancy of tial irritants. In addition, we aimed to evaluate the sensitivity of rimental techniques for investigating repellancy. Allyl isothiocya- erine, and mercaptobenzoic acid were offensive to both red-wings ngs: ammonia, gingerol, and zingerone were apparently innocuous. atter substances, the lack of repellant effects lends support to the at there are functional differences between the mammalian and eminal systems. The factors which account for this discrepancy re- lear, but avian trigeminal receptors may lack the appropriate struc- ract with at least some irritants (Szolcsanyi et al., 1986).

lyl isothiocyanate, piperine, and mercaptobenzoic acid, observed y was dependent on the manner of presentation. When birds ex- all compounds at only one concentration (experiment 3), even the el of each chemical (0.001%) was aversive. Conversely, when birds red all concentrations of only one compound (experiments 1 and 2), highest concentrations (≥1.0%) were effective, and starlings ap- ore sensitive than red-wings. These discrepancies are not readily in biological or behavioral terms. However, they do highlight dif- n the efficiency of the changeover design (experiment 3), relative rd repeated concentrations designs (experiments 1 and 2). In ex- 3, the error mean square for testing among species, concentrations, s, and higher order interactions was 0.32, and the standard error ment mean was 0.23. In experiment 2, the error mean squares for eatment and concentration means were 1.29 and 0.29, respectively. g 12 birds per group as in experiment 3 (for the purpose of compar- n the standard errors of treatment and concentration means in ex- 2 were 0.33 and 0.15, respectively. Given these standard errors, repeated concentrations design was about 50% more sensitive (0.23/0.15) than the changeover design in detecting differences among concentration means. Ignoring the possibility that carryover effects may have confounded the results of experiment 2, then a reasonable conclusion is that the changeover design sacrificed some power in detecting concentration differences for increased power in detecting differences among treatments (irritants).

Residual effects apparently did not play a significant role in experiment 3. Thus alternative changeover designs that do not assume the presence of such effects should be considered (cf. Federer, 1955, p. 441) in experiments aimed at isolating differences among irritants. Such designs are probably more powerful than the changeover design used in experiment 3 because more degrees of freedom are available for estimating experimental error.

V. MANAGEMENT IMPLICATIONS

Allyl isothiocyanate, piperine, and mercaptobenzoic acid were offensive to birds in the present experiments. Of these, allyl isothiocyanate was the most effective. We speculate that any of these materials might serve as bird repellants in particular situations. For example, allyl isothiocyanate, perhaps incorporated into a paste, might be used as a fumigant to disperse birds from enclosed structures. In addition, starling and blackbird depredations at swine and cattle feed lots (Feare, 1975, 1980) can be reduced through the use of feeds that are unpalatable to birds but acceptable to livestock (Glahn and Mason, unpubl. data). Piperine is already added to swine feeds to improve "mouth feel" at the rate of 0.05-0.15% (w/w) (Cerny and Bazucha, 1983). The present experiments suggest that piperine may also have value as a bird repellant feed additive. In either case, the fact that these substances possess fungicidal and insecticidal properties (Matsurbara and Tanimura, 1966; Su, 1977; Madhyastha and Bhat, 1984; Das et al., 1985; Das and Choudhury, 1984; Nakatani et al., 1986) suggests that they may also act as preservatives of the baits into which they are incorporated. Finally, in experiment 1, gingerol was not offensive at any concentration. While this may (in part) reflect the insensitivity of the paradigm used in experiment 1, there is no evidence that low concentrations of gingerol are detected by birds. For mammals, gingerol (and piperine) enhances the uptake of substances from the gut (Atal et al., 1985). Conceivably, gingerol could produce the same effect in the avian gut without reducing overall food intake. As such, gingerol might be used to enhance the effectiveness of poultry feed additives and medications, and for pest birds, to improve the potency of ingested toxicants.

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Chapter 15 Discussion

Dr. Rozin: I may have missed something along the way, but are all the tests you showed us consumption tests?

Dr. Mason: Yes. All the laboratory tests involve consumption.

Dr. Rozin: Is it consistent with what you found that there is no real nasal irritation sensitivity at all in these animals? That is to say, that all of the results could be due to the oral cavity.

Dr. Mason: With the exception of the first two slides where we plugged the nose and the responding is abolished, in that particular experiment I would argue that it's a nasal capsule effect. It could be oral acceptance when we cut olfactory nerves and trigeminal innervation of the nasal capsule but not the oral cavity. We do find these selective effects.

Birds are very much like amphibians; unlike mammals they have long olfactory nerves that can be sectioned. You can do the same thing with trigeminal innervation of the nasal capsule. Interestingly enough, Wayne Silver and I tried for some time to get trigeminal nerve recordings from starlings and I think, Wayne, you only got occasional units that responded to odor?

Dr. Silver: Yes.